VARIATION IN SNOW GUM (*EUCALYPTUS PAUCIFLORA* SIEB.)

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(Plates xv-xvi; two Text-figures.)

[Read 28th November, 1956.]

Synopsis.

Variation in Snow Gum (*E. pauciflora* Sieb.) populations is described. In continuous stands, linear correlation between a number of characters and elevation is found. Genotypic variation is found to accompany phenotypic variation. Heritable variation is found likewise in stands which occur separately over wide areas. The Snow Gum population varies clinically in several directions showing correlation with habitat variation and it is implied that such a variation has adaptive value. Taxonomically it is considered that the whole population should be regarded as one species and referred to *E. pauciflora* Sieb. The term "cline-form" is proposed for a reference point within any part of the population, and it is considered that *E. niphophila* Maiden and Blakely, *E. de Beuzevillei* Maiden and *E. pauciflora* Sieb. var. *nana* Blakely should be suppressed and regarded not as species or varieties but as cline-forms. Many *Eucalyptus* species exhibit in some degree the same kind of variation.

Eucalyptus Populations.

On distribution maps it is the custom to show species of *Eucalyptus* which have a wide geographic range as occupying relatively few and often large, continuous areas.

This is, in all but a very few cases, a considerable over-simplification. *Eucalyptus* species usually occupy quite sharply limited ecological situations and, while there may be numerous repetitions of the site which carry the particular species, each is usually surrounded by other sites supporting different species, so that a closer approximation to fact would be to show, if practicable, a large number of distinctly separate stands through the general area of distribution of the species.

In most species it is obvious that there is phenotypic divergence in such separate stands, and it is clear that this is accompanied as a rule by parallel genotypic difference. What is more, in *Eucalyptus* it may well be that Clausen's (1951) comment is applicable, namely, that genetically controlled physiological divergence between different populations of the same species is present at the same time, or even before any character detectable in the phenotype. The degree of difference between any pair of stands is generally related to the distance by which they are geographically separated, and more especially to the extent to which the two sites differ in some broad, changing environmental feature such as is correlated with altitude or latitude change. It is likely that separate stands are often largely interbreeding populations, each isolated to a considerable degree from the other.

This distribution pattern fits Snow Gum (which is usually referred to as *Eucalyptus pauciflora* Sieb.) in some of its range, but only partly so, because this species is one of the few exceptions within the genus which also covers quite large geographic areas which it continuously occupies. *E. pauciflora, sensu lato*, not only occurs in disjunct stands through a wide area, but also forms pure stands on the highlands of south-eastern Australia above about 4,000 feet, and all the areas between about 5,000 and 6,000 feet elevation in this part of the country are occupied almost exclusively by the species.

It therefore offers an opportunity for study of the variation which accompanies two patterns of distribution in a *Eucalyptus* species. In studying the stands of *E. pauciflora* at high elevations, this epithet is taken to embrace the species *E. niphophila* Maiden and Blakely and *E. de Beuzevillei* Maiden, both of which can be regarded as part of *E. pauciflora* Sieb., according to a viewpoint, which will be elaborated below.

Variation in a Continuous Stand.

The Brindabella Range, Australian Capital Territory, was selected for the examination, since the species occurs continuously between 4,000 and 6,000 feet over a distance of 20 miles, and extends well beyond this too. By inspection, there is an obvious correlation between the height of the dominants of the stand and the elevation at which it is growing; the stands from high elevations are short or even dwarf, while those at 4,000 feet are from 70 to 90 feet tall (Plate xv, *a-e*). To establish whether such a correlation is heritable, or merely the result of direct environmental action on the individual to alter the phenotype, requires experiment. A number of other characters can easily be seen to vary with altitude, but the degree and nature of the correlation is too difficult to assess without metrical study. These characters therefore were examined statistically.

Method.

Five sites were chosen in saddles on the Brindabella Range (as this presented an essentially similar physiographic situation in each case), separated by approximately 500 feet elevation. Five dominant trees were taken at each site and measurements made of the maximum total height of the stand, bark thickness, fruit diameter and leaf length. Open pollinated seed was collected from each tree, and a progeny raised from each. Subsequently, growth of the progenies was measured after one year in tubes in the nursery, and then some were planted out at different elevations, viz.: 5,500 feet, 4,000 feet and 2,000 feet.

Various precautions were taken to make the measurements in each case as nearly comparable as possible. Bark thickness was made at breast height with a bark gauge taking the average of four readings, one in each quadrant of the trunk. The maximum fruit diameter was measured in each case, and these were confined to the same fruit crop. Ten capsules were measured from each tree.

In measuring leaf length attention must be given to the morphology of the short leaf-bearing shoot. On mature trees of *E. pauciflora* growing at 4,000 feet or above, the short leaf-bearing shoot usually consists of about four or five somewhat separated pairs of leaves (Jacobs, 1955). The leaf shape and size follow a sequence from the first pair, which are relatively small and rather short in relation to length, through successive pairs to a maximum beyond which they diminish again in size. This shoot represents one growing season. The third pair of leaves is usually the longest and in each case the longest leaf on the shoot was measured. Ten measurements were made on each tree.

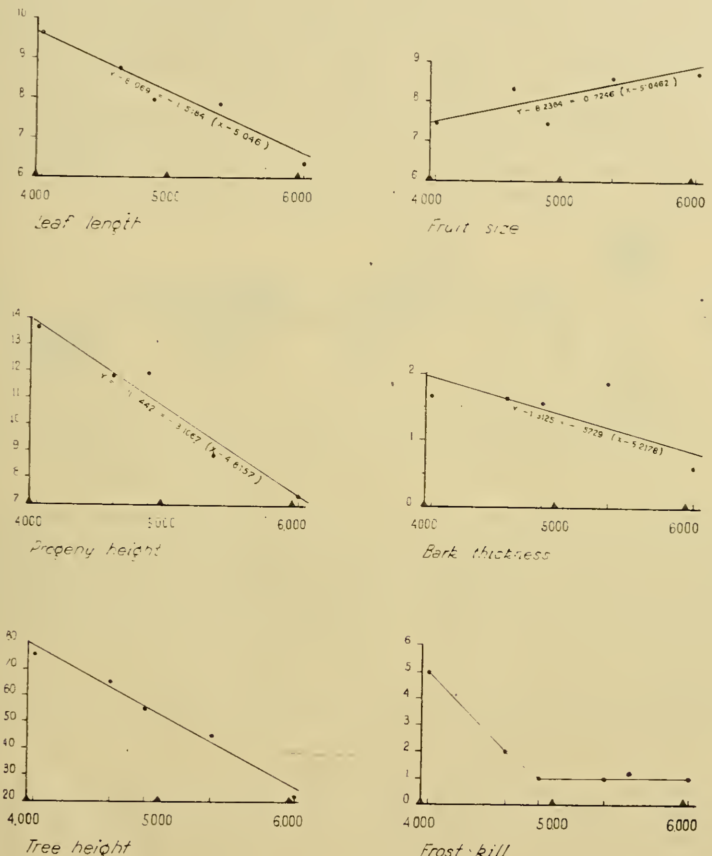
In the progeny tests, sowings were made with seed from all trees, but in some cases the plants were lost, and in others they were relatively few; nevertheless, the numbers were sufficiently large to permit examination of some aspects of progeny character in relation to parental character.

The capacity to withstand low temperatures was tested by planting five individuals from each group of the trees in the original stands at different elevations, one of which was 5,500 feet, near the upper altitudinal limit where the frosts were near the extreme experienced by the species.

Results.

The results of the measurements and trials are set out graphically in Text-figures 1 and 2. The most obvious correlation is that of tree height with elevation. There is a very regular fall-off in height as one ascends, the correlation being closely linear. Such a variation might at first seem entirely phenotypic, and could be a direct effect of environment on the plant without corresponding genotypic gradation. However, the correlation of progeny height (based on growth in the nursery for one year) with elevation of origin is also linear and high. This implies that the rate of growth of seedlings in the first year is correlated with the elevation of seed source, and therefore it is highly probable (especially since it is known from less precise experiments that reduced growth rate is maintained for the first eight years of growth) that this is maintained throughout the life of the tree, and the total height which the tree reaches at any age in the environment of the experimental garden or in any given particular environment is in a large measure genetically determined.

In testing the capacity to withstand frost, although the numbers involved in the trial are few, it is obvious also that this is closely related to the origin of seed since, when they are all planted at a high elevation, those from high elevations are able to withstand temperatures which kill seedlings from plants from lower elevations. A second test with the same material carried out near Rules Point by R. M. Moore (1955) leads to a similar conclusion.



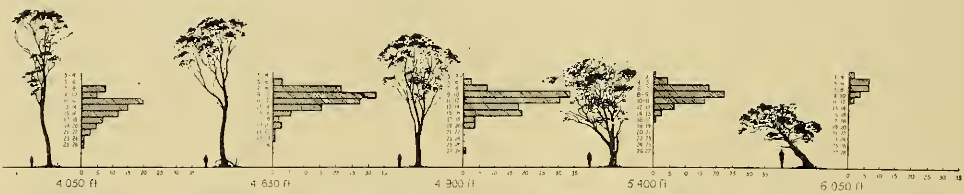
Text-fig. 1.—Showing correlation between elevation and leaf length, fruit size and bark thickness and total height on the mature trees, and also the correlation between progeny height at 1 year of age and killing by frost. Leaf length: cm.; fruit size (diam.): mm.; bark thickness: inches; progeny height: inches at 12 months; tree height: feet; frost kill: number killed out of 5 planted from each stand sampled.

In all the characters measured there are gradual changes and, except for bark thickness where there is significant residual variance, there is linear correlation of high significance between these characters and elevation. It is seen that at the higher limits the trees are shorter in total height, with shorter leaves, larger fruit, thinner bark, greater resistance to low temperature, and giving progeny with slower rate of growth. It is obvious that slower growth and greater frost resistance are strongly adaptive characters. This can easily be explained, as faster growth in this case means a longer growing season, and the initiation or continuation of growth beyond the normal time for trees in a cold area would make an individual more susceptible to early or late frost, which is a feature of the higher elevations. Such individuals would tend to be eliminated by simple environmental selection, since they would be in a more susceptible condition to early and late frosts.

On the other hand, where there is simply superior physiological resistance to low temperatures, those individuals which cannot withstand the temperatures ordinarily experienced at the higher elevations would be killed outright, or so retarded that they would be lost in competition with the more effective but slower growing individuals.

With regard to the other characters examined, it is also easy to imagine that shorter leaves would be able to withstand the stronger winds at higher elevations and the more severe icing if only because of the mechanical advantage which they possess, and therefore it seems this is of adaptive value. The adaptive significance, which indeed it seems must be so, of fruit size and bark thickness is not apparent at first sight, and it might seem, for example, that the thin bark would be less satisfactory for survival at higher elevations than thicker bark.

There are other characters which are probably of adaptive value, such as glaucousness. This increases with elevation in a manner comparable with that described by Barber (1955) for some Tasmanian species, but it is not so easily susceptible to measurement and has not been examined in detail in this case.



Text-fig. 2.—Histogram showing the progeny height in inches of all the plants raised from each stand at the elevations indicated The form of the parent tree is indicated in silhouette. The number of plants in each height class is indicated on the horizontal axis.

It is apparent that populations of *E. pauciflora* on the Brindabella Range, though continuous and graded in accordance with elevation, and showing close linear correlation with elevation of a number of characters, are at any point in some degree genetically heterogeneous. Irregularities in trees at a particular site in fruit size, frost resistance and other characters point to a degree of heterozygosity for these characters in any particular stand.

The general conclusion from these facts is that most characters of *E. pauciflora* vary continuously in stands above 4,000 feet elevation without any discontinuity, and that they are closely correlated with habitat.

Variation in Disjunct Stands.

E. pauciflora, in addition to the type of stand described above, occurs as many quite small separated stands from near the Queensland border through New South Wales and Victoria to the South Australian border, and in Tasmania. It is a species of the colder areas, and is frequently found on the tops of hills or ranges, so that as these are often of small extent the stands are small and well separated from each other. On the southern tablelands also there is a distinct habitat formed by cold air drainage, which leads to the development of frost hollows (Pryor, 1954; Moore, 1955). These frost hollows, when conditions are not too extreme for trees, carry *E. pauciflora*, which is evidently the species best able to withstand such conditions. Frost hollows are separated one from the other so that there is a disjunct habitat distribution which is comparable with that of the hilltops. This also leads to separate stands of relatively small extent occurring in different areas. The form of *E. pauciflora* in the more extreme frost hollows of the Monaro area of New South Wales is pendulous and very distinct from other forms of the species.

Five collections of *E. pauciflora* were made from disjunct sites, as follows: Mt. Hotham, Victoria (about 5,500 feet); Kybean Peak on the Dividing Range east of Cooma (about 4,000 feet); Numeralla (Murrumbidgee Valley, 40 miles south of Canberra, about 2,400 feet); Bright Valley, Victoria (about 1,500 feet); and a frost hollow near Adaminaby (about 3,000 feet elevation). Progeny was raised from each of these and planted out. At six years of age the rate of growth has differed widely in progeny from the different collections, and an analysis of variance of height growth leads to the results in Table I, showing the differences in means which in all but one case are significant.

TABLE 1.

Locality.	Number of Plants.	Mean Height (In.).
1. Adaminaby (frost hollow)	3	251·67
2. Hotham	10	69·61
3. Kybean	44	142·26
4. Numeralla	49	180·17
5. Bright	61	144·78

Differences of Means.

	No. 3.	No. 5.	No. 4.	No. 1.
No. 2	72·65[3]	75·17[3]	110·56[3]	182·06[2]
No. 3	—	2·52	37·91[3]	109·41[1]
No. 5	—	—	35·39[2]	106·89[1]
No. 4	—	—	—	71·50[1]

[1] Significant at 0·05 level.
[2] ,, ,, 0·01 ,,
[3] ,, ,, 0·001 ,,

There are many other differences besides rate of growth, some of which are not so easy to measure. Some are relatively minor differences, such as colour of the leaf-bearing stems, which, for example, in the Kybean population is consistently dark red. The leaves of the Bright Valley form are coarser and larger than the others, whereas the Adaminaby form is a very markedly pendulous type with the habit of the Weeping Willow, narrow leaves and very glaucous stems (Plate xvi). The characters within each progeny are relatively uniform, but they are sharply distinct from the progenies from other areas. The same is true of the parent stands. This indicates, therefore, that the phenotypic differences are supported by corresponding genotypic differences, and that these variations seen from stand to stand are strongly inherited. It will be noted that the correlation of rate of growth with altitude of origin applies generally only to stands from higher elevations, and that as one descends to lower elevations, say below 4,000 feet, other factors beside elevation come into the relationship and it no longer holds.

The pendulous form in frost hollows does not in single cases show the graded sequence to the surrounding more common form of *E. pauciflora*, as is the case with graded variation described above in the continuous stands at higher elevations. The transition is a sharply graded cline—occupying a zone of 100 yards or so. However, if one seeks situations where the frost hollows are less extreme a series of stands can be found which can be arranged in clinal sequence for the character of pendulous habit. Thus the pendulous form, although often relatively isolated in any given situation from the surrounding stand of *E. pauciflora*, is clinally connected with that stand and with the whole population in the variation pattern of the species.

Taxonomic Treatment.

Taxonomic treatment according to the classical basis is unsatisfactory if applied to such a population. The whole is rather distinctly cut off from other species within the genus, and if the type specimen *E. pauciflora* Sieb. is applied to the whole population and this is regarded as the species, this is satisfactory as far as it goes. The degree of variation is such, however, that it is important to know more about it, and taxonomic attempts to describe it have been made by selecting types from different points within the population and erecting them as species. Two such species and one variety have been thus erected—*E. niphophila* Maiden and Blakely, *E. de Beuzevillei* Maiden and *E. pauciflora* Sieb. var. *nana* Blakely. There are two other forms which are equally distinct from *E. pauciflora* Sieb., but they have not been described. For the purposes of discussion they might be referred to as "*montana*", which is the 80-feet forest tree occurring at 4,000 feet on the Brindabella Range, and "*pendula*", which is the frost-hollow form near Adaminaby. If on this basis an attempt is made to classify any particular stand or individual of the *E. pauciflora* population, there is an immediate difficulty. For example, *E. niphophila* is the upper altitudinal end-point of the cline of *E. pauciflora* on Mt. Kosciusko, having been described from near the old hotel site. As one descends, there is the same kind of correlation characteristic of the continuous stand on the Brindabella Range, so that the other terminal point is the "*montana*" form. The *montana* form is, in the herbarium, distinctly closer to *E. pauciflora* Sieb. than it is to *E. niphophila*, although if field characters are taken into account it is equally distinct. It is clear, then, that any determination of the limits of *niphophila* will be highly subjective, and it is not likely that any two systematists will give the same answer, since there is no precise boundary to the stands, or no discontinuity which might be referred to as the limits of *niphophila*. Likewise, *de Beuzevillei* is the upper altitudinal end-point of the cline of *E. pauciflora* on the Jounama Range. The Jounama Range is distinctly more continental in its environment than the Kosciusko Range. This is reflected in the character of the population. If a series of ranges is considered, such as Mt. Kosciusko, Brindabella Range and Jounama Range, the forms of *E. pauciflora* at the tree line in each case (that is the end-point of each cline by which each is connected to the *montana* form of *E. pauciflora*) are themselves clinally arranged (though perhaps "stepped") according to increasing "continentality". The position is only apparently simpler with the disjunct stands which go to make up the remainder of the *E. pauciflora* species population since, if enough stands are considered, although there is a tendency for the gradation between stands to be stepped so that there are small discontinuities, the magnitude of these discontinuities is found to be reduced continually the more stands that are considered, and there are so many separate stands that there is no effective difference between those exhibiting continuous variation and those occurring as separate stands.

Where stands at first appear discontinuous, as where a sharp habitat change, such as frost hollow site carrying "*pendula*" changes over abruptly to a more usual tableland site carrying a population nearer the type, *E. pauciflora* Sieb., it is found by examining a series of frost hollows each less intense than the last that they are connected clinally.

It is clear, therefore, that if *E. pauciflora* Sieb. is "split" in the taxonomic sense by erecting a series of species based on single type specimens, very considerable confusion develops. On the other hand, if the described species and variety *E. niphophila*, *E. de Beuzevillei* and *E. pauciflora* var. *nana* are suppressed and "lumped" into *E. pauciflora* Sieb., the population is still not adequately described. Classical taxonomy uses a single type specimen to define the species and then subjective opinion of the taxonomist determines which other individuals and populations will be related to the species. If the described types could conveniently be taken to represent populations of *E. pauciflora* in distinct geographic areas, and without gradual intergradation, they could well be regarded as subspecies, as can apply perhaps in some cases with other species of *Eucalyptus*. Since the various populations lack distinct boundaries, however, the erection of these types as subspecies does not help classification. The variation of *E. pauciflora* is multi-dimensional and for all practical purposes continuous. While ultimately it may be possible to use some metrical system for defining the species which would allow precise description of continuously varying systems, the most practical way at the moment of treating the population is to preserve the type *E. pauciflora* Sieb., as representing the species, and to use the other described forms and any which it may be considered worth while adding from time to time as points of reference within a population for aiding description.

A term is needed in *Eucalyptus* taxonomy to refer to types within the total species population which are to be used as such reference points. Neither the term "subspecies" nor "variety" will meet the case, the former for the reasons mentioned above, and the latter because it has been applied in too many different ways in botanical study (Clausen, 1941). It is proposed, therefore, that the term "cline-form" be used. *E. pauciflora* Sieb., therefore, has three described cline-forms—*niphophila*, *de Beuzevillei* and *nana*—which are arrived at by suppressing the species *E. niphophila* Maiden and Blakely, *E. de Beuzevillei* Maiden and variety *E. pauciflora* Sieb. var. *nana* Blakely. To these might well be added for convenience the yet-to-be-described forms "*montana*" and "*pendula*". Taxonomically, then, any stand of Snow Gum is at once conveniently referred to the species *E. pauciflora* Sieb. When more precision is required, as it is for many purposes, a particular stand can be referred to its position in relation to cline-forms, e.g., approaching or identical with cline-form *niphophila*, or between two cline-forms, as the case may be. There is no need to limit the number of cline-forms to be described; the number would simply be determined as that necessary for adequate description of the population.

Acknowledgements.

Grateful acknowledgement is made to Mr. G. A. McIntyre for the statistical comparisons, to Mr. O. Ruzicka for the drawings, and to Mr. W. Pedersen for the photographs.

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EXPLANATION OF PLATES XV-XVI.

Plate xv.

a, b, c, d, e: *E. pauciflora* on the Brindabella Range from 4,000 to 6,000 feet elevation, each stand separated by approximately 500 feet elevation from the adjoining one.

Plate xvi.

a, b, c, d, e: 6-year-old plants from Snow Gum from different localities: *a*: Mt. Hotham; *b*: Kybean; *c*: Numeralla; *d*: Bright Valley; *e*: Frost hollow, Adaminaby.